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Long-term organic farming fosters below and aboveground biota: Implications for soil quality, biological control and productivity

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ABSTRACT

Organic farming may contribute substantially to future agricultural production worldwide by improving soil quality and pest control, thereby reducing environmental impacts of conventional farming. We investigated in a comprehensive way soil chemical, as well as below and aboveground biological parameters of two organic and two conventional wheat farming systems that primarily differed in fertilization and weed management strategies. Contrast analyses identified management related differences between “herbicide-free” bioorganic (BIOORG) and biodynamic (BIODYN) systems and conventional systems with (CONFYM) or without manure (CONMIN) and herbicide application within a long-term agricultural experiment (DOK trial, Switzerland). Soil carbon content was significantly higher in systems receiving farmyard manure and concomitantly microbial biomass (fungi and bacteria) was increased. Microbial activity parameters, such as microbial basal respiration and nitrogen mineralization, showed an opposite pattern, suggesting that soil carbon in the conventional system (CONFYM) was more easily accessible to microorganisms than in organic systems. Bacterivorous nematodes and earthworms were most abundant in systems that received farmyard manure, which is in line with the responses of their potential food sources (microbes and organic matter). Mineral fertilizer application detrimentally affected enchytraeids and Diptera larvae, whereas aphids benefited. Spider abundance was favoured by organic management, most likely a response to increased prey availability from the belowground subsystem or increased weed coverage. In contrast to most soil-based, bottom-up controlled interactions, the twofold higher abundance of this generalist predator group in organic systems likely contributed to the significantly lower abundance of aboveground herbivore pests (aphids) in these systems. Long-term organic farming and the application of farmyard manure promoted soil quality, microbial biomass and fostered natural enemies and ecosystem engineers, suggesting enhanced nutrient cycling and pest control. Mineral fertilizers and herbicide application, in contrast, affected the potential for top-down control of aboveground pests negatively and reduced the organic carbon levels. Our study indicates that the use of synthetic fertilizers and herbicide application changes interactions within and between below and aboveground components, ultimately promoting negative environmental impacts of agriculture by reducing internal biological cycles and pest control. On the contrary, organic farming fosters microbial and faunal decomposers and

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this propagates into the aboveground system via generalist predators thereby increasing conservation biological control. However, grain and straw yields were 23% higher in systems receiving mineral fertilizers and herbicides reflecting the trade-off between productivity and environmental responsibility.

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1. Introduction

Long-term agroecosystem experiments provide an indispensable resource for the evaluation of effects of farming systems on soil quality, above and belowground biota and productivity (Rasmussen et al., 1998). However, little is known about the integral consequences of organic versus conventional farming systems, as those components are traditionally studied in isolation (for reviews see Bengtsson et al., 2005). This study investigates effects of four farming systems on soil chemistry, microorganisms, soil and aboveground fauna and productivity of winter wheat fields in a long-term agricultural experiment (DOK trial, Switzerland).

Agroecosystems are highly productive systems with open nutrient cycles. They lose nutrients through runoff, leaching, denitrification, removal of crop residues and harvest and consequently depend on continuous nutrient inputs to compensate for nutrients' losses (Tivy, 1987). Such losses probably affect lower trophic levels with expected consequences for different ecosystem services (e.g. pest suppression, Letourneau and Bothwell, *in press*). Long-term application of organic fertilizer indeed results in an increase in the carbon content of soils (Fließbach et al., 2007) and in a resource-mediated promotion of bacteria (Fließbach and Mäder, 2000) and arbuscular mycorrhiza (Oehl et al., 2004) in the DOK trial. This, in turn, likely affects the soil fauna and alters the decomposition of crop residues and hence the availability of nutrients (Lundquist et al., 1999). The effect of allochthonous resource input on soil fauna may further influence aboveground animal communities as increased carbon availability may cascade up to higher trophic levels (Halaj and Wise, 2002). Surface-active predators may benefit from increased prey availability from the belowground subsystem ("energy shunt hypothesis"; Oksanen et al., 1997), either improving (Scheu, 2001) or reducing (Birkhofer et al., 2008a) pest suppression by natural enemies. As mineral (NPK) fertilizer application may reduce (Ryan, 1999) or increase soil organic matter levels (Rasmussen et al., 1998) it is important to understand cascading effects of bacterial and fungal growth on higher trophic levels of the soil food web (Wardle, 2002). In the DOK trial Birkhofer et al. (*in press*) indeed found generalist predators in grass-clover plots to be affected by fertilization strategies. Considering the increased attention that sustainability of farming practices receives, the lack of thorough studies on effects of different farming systems on below and aboveground biota is unfortunate.

Using the DOK experiment design we evaluated differences between the following farming systems: (i) conventional and organic farming, (ii) stockless farming and mixed farming, (iii) conventional farming with livestock and organic farming, (iv) stockless conventional farming and mixed farming and (v) organic farming with composted and with rotted farmyard manure. We expected farmyard manure application to positively affect soil quality, nutrient cycling, microorganisms and decomposer animals. We further hypothesized that these belowground changes propagate into the aboveground food web via generalist predators thereby increasing pest control.

2. Material and methods

2.1. Study site and experimental design

The DOK trial in Therwil, Switzerland is a long-term agricultural experiment established in 1978 by the Agroscope Reckenholz-

Tänikon research station (ART) and the Research Institute of Organic Agriculture (FiBL). The soil is a haplic luvisol on deep deposits of alluvial loess. Mean precipitation is 785 mm per year with an annual average temperature of 9.5 °C (Mäder et al., 2002).

We analyzed wheat plots of two organic farming systems (BIODYN, BIOORG), one conventional (CONFYM) system, receiving farmyard manure, and a second conventional system mimicking stockless farming (CONMIN, receiving mineral fertilizers only; see Table 1) in May 2005 when plant growth is vigorous and soil microflora and fauna are active and therefore likely reflect differences between farming systems. Further, potential biocontrol effects of generalist predators most likely occur early in the season.

Crop rotation and soil tillage regime were identical for all 5 × 20 m large plots. Synthetic insecticides were last applied in 2001 in the conventional systems and soils of the CONFYM and CONMIN system were treated with a molluscicide in 2003 and 2004. A single herbicide containing the active ingredients carfentrazone and isoproturon was applied to winter wheat in both conventional systems on 1 April 2005 and the growth regulator trinexapac-ethyl was applied on 22 April 2005. The two conventional systems received a total of 90 kg N ha⁻¹ as calcium ammonium nitrate in March and April 2005, BIOORG received a total of 44 m³ slurry ha⁻¹ in two rates (N_{tot} 77.9, N_{min} 33.2, organic matter 1335 kg ha⁻¹) and BIODYN 30 m³ ha⁻¹ (N_{tot} 46.2, N_{min} 28.5, organic matter 651 kg ha⁻¹) only once.

2.2. Soil sampling

All four replicated wheat plots of each farming system were sampled on 9 May 2005 by collecting seven small soil cores (diameter 8 cm, depth 5 cm), one large soil core (diameter 20 cm, depth 5 cm) and one sample of bulk soil (1 kg) from the upper 5 cm layer of randomly chosen locations at the northern and southern end of each of the plots (minimum edge distance 1.5 m). Bulk soil was used to analyze chemical soil properties and microbial parameters; soil cores or homogenized soil from soil cores (Nematodes) were used to analyze soil fauna.

2.3. Soil chemistry

Soil pH was measured in 0.1 M KCl solution in a soil to liquid ratio of 1:3 (w/v). Total soil nitrogen and carbon were measured using an elemental analyzer (Carlo Erba, Milan, Italy) and were taken to represent total soil nitrogen content (N_{tot}) and soil organic carbon content (C_{org}), as concentrations of carbonates are generally low at the study site. To measure soil water content fresh soil samples were dried at 105 °C for 72 h.

2.4. Microorganisms

To measure soil microbial biomass soil samples were sieved (2 mm mesh) and the water content was adjusted to 50–60% maximum water holding capacity. One week before analysis, soil samples were pre-incubated at 20 °C. Soil microbial biomass C (C_{mic}) and N (N_{mic}) were measured by chloroform-fumigation-extraction (CFE) according to Vance et al. (1987).

The abundance of bacteria and fungi was estimated using direct counting and phospholipid fatty acid (PLFA) analysis. Direct

microscopic counts of bacteria and fungi were performed on soil smears (Bloem and Vos, 2004). Slides for bacterial counts were analyzed following Bloem et al. (1995). Bacterial biomass carbon was estimated from the biovolume using a carbon content of $3.1 \times 10^{-13} \text{ g C } \mu\text{m}^{-3}$. Slides for fungal counts were stained with differential fluorescent stain, a mixture of europium chelate (stains nucleic acids red) and fluorescent brightener (stains polysaccharides in cell walls blue). Unstained fungal hyphae visible with transmitted light were included in the counts. Total hyphal length was measured using the grid intersection method and an epifluorescence microscope at $400\times$ magnification. Biovolume was calculated using the equation $V = (\pi/4)W^2(L - W/3)$, where W = hyphal width (μm) and L = hyphal length (μm). Fungal biomass was calculated assuming a mean hyphal diameter of $2.5 \mu\text{m}$ and a specific carbon content of $1.3 \times 10^{-13} \text{ g C } \mu\text{m}^{-3}$.

Lipid extractions for analysis of PLFAs and NLFAs were made on 3 g of fresh soil according to Frostegård et al. (1993) and Hedlund (2002). The resulting fatty acid methyl esters were separated on a Hewlett Packard 6890 gas chromatograph. Relative retention times of the fatty acid methyl esters were compared to those of standards. The sum of the PLFAs i15:0, a15:0, 15:0, i16:0, 16:1 ω 9, i17:0, a17:0, cy17:0, 18:1 ω 7, and cy19:0 was used as an index of bacterial biomass (Frostegård and Bååth, 1996). The amount of PLFA 18:2 ω 6 was used as an index of non-mycorrhizal fungal biomass and NLFA 16:1 ω 5 as a marker for arbuscular mycorrhizal fungi (Olsson, 1999; Hedlund, 2002).

Microbial basal respiration was measured using an automated respirometer system based on electrolytic O_2 -microcompensation (Scheu, 1992). Samples were pre-incubated for 1 week at 20°C and 40–50% of their maximum water holding capacity and subsequently analyzed. For basal respiration, the average O_2 consumption rate ($\mu\text{l O}_2 \text{ g}^{-1} \text{ h}^{-1}$) of samples not amended with glucose during hours 10–20 after attachment to the respirometer system was used. The specific respiration ($q\text{O}_2$; $\mu\text{l O}_2 \text{ mg}^{-1} \text{ C}_{\text{mic}} \text{ h}^{-1}$) was calculated from data on microbial biomass (C_{mic}) and basal respiration.

Microbial activity of the different soils was estimated by indices calculated from the capacity of the microbial biomass to utilize ^{14}C glucose added to the soil (for details see Nguyen and Henry, 2002). The microbial growth parameter (A) describes the fraction of the added ^{14}C that is mineralized during the rapid mineralization phase. The microbial maintenance parameter (C) represents the fraction of added ^{14}C that was mineralized at the end of the slow mineralization phase. Potential nitrogen mineralization rate in soil was determined by incubating 200 g soil samples at 20°C and about 50% water holding capacity for 6 weeks. Water holding capacity was determined following Forster (1995) and water content was analyzed before and after incubation. N mineralization rate

was calculated from the increase in mineral N concentration between week 6 and week 2, excluding data from week 1 to reduce any effect of sample handling. This method showed good agreement with *in-situ* measurements of N mineralization (Bloem et al., 1994). Recently, Curtin et al. (2006) evaluated different methods and found that aerobic incubation at 20°C and optimum water content was the best predictor of plant N derived from mineralization.

2.5. Soil fauna

The abundance of heterotrophic flagellates and naked amoebae was estimated using the most probable number method (Rønn et al., 1995). Samples of soil (about 1 g fresh wt) from each replicate plot were mixed with 20 ml of 'Modified Neff's amoeba saline' (Page, 1988) and subsequently blended for 1 min in a Waring Laboratory Blender (7012S) at 22,000 RPM. A threefold dilution series in Costar (3598) microtiter plates (8 replicates of 12 dilutions) was then amended with 100 μl of Tryptic Soy Broth (0.1 g l^{-1} ; Difco Bacto, Detroit, Michigan, USA). The plates were stored in darkness at 10°C and analyzed for the presence of protozoa after 1 and 3 weeks incubation using an Olympus inverted microscope (IMT-2).

Nematodes were extracted from 120 g subsamples of soil using Oostenbrink elutriators (Oostenbrink, 1960), killed by heat and fixed (35% formaldehyde diluted to 4%). The total number of nematodes was counted and a minimum of 150 nematodes were further identified to family or genus level according to Bongers (1988) and allocated to feeding groups according to Yeates et al. (1993).

Enchytraeids were extracted from soil using a combination of cold and hot wet funnel extraction methods to maximize the extraction efficiency. A soil sample was first submerged in cold water for 24 h in a plastic sieve following the protocol in Dunger and Fiedler (1997), and later heated for 3–4 h in a wet funnel following the protocol of O'Connor (1955). The individuals were identified to species or genus level. Other soil animals were extracted from one large (20 cm diameter; macrofauna) and three small soil cores (5 cm diameter; mesofauna) using a modified heat extraction system (Kempson et al., 1963). Samples were stored in 70% ethanol for later identification.

2.6. Aboveground fauna and vegetation

The vegetation-based fauna was sampled on May 16 under dry conditions using an Eco-Vac insect suction sampler (EcoTech, Bonn, Germany). An area of 0.7 m^2 was fenced on each of the two sides of each plot (PVC barriers, 50 cm high) and immediately suction sampled for 90 s. Samples were transferred to glass vessels

Table 1
Farming systems established in the DOK trial in Therwil, Switzerland

Treatment name	Biodynamic	Bioorganic	Conventional	Mineral
Abbreviation	BIODYN	BIOORG	CONFYM	CONMIN
Organic fertilizer	Composted FYM	Rotted FYM	Stacked FYM	-
Inorganic fertilizer	-	-	NPK	NPK
Weed control	Mechanical		Mechanical & chemical	
Disease control	Indirect methods		Chemical (threshold)	
Pest control	Plant extracts		Chemical (threshold)	
Special treatments	BIODYN prep.	-	Plant growth regulators	
Nutrients ($\text{kg ha}^{-1} \text{ yr}^{-1}$)				
$\text{C}_{\text{organic}}$	1818	2272	2272	0
N_{total}	99	102	157	122
$\text{N}_{\text{mineral}}$	31	35	101	122
P	23	27	41	40
K	165	157	258	250

Terms and abbreviations given in this table are used throughout the text. Fertilizer (farmyard manure = FYM, inorganic = NPK) and mean annual nutrient amendments between 1978 and 2005 to all systems during four crop rotation periods. Table modified from Fließbach et al. (2007). Note that the conventional systems are farmed according to Integrated Plant Production Standards (IPP).

containing a small amount of ethyl acetate. Suction samples were stored at -10°C and later sieved and hand sorted using a dissecting microscope (Leica MZ12) to separate animals from debris. To estimate densities of surface-active animals an area of 2.0 m^2 was fenced (PVC barriers; 50 cm high, 10 cm sunk into the soil) and four pitfall traps containing a water detergent mix were placed along the inner barrier and left open for 14 days (May 3–17). Pitfall samples were transferred to 70% ethanol, sieved and later hand sorted. To analyze effects of different farming regimes on the diversity of below and aboveground fauna, species richness, Shannon–Wiener diversity index and evenness index were calculated for nematodes, enchytraeids, spiders and carabids in each plot.

Yield was estimated on July 23 from a centre plot of $1.7 \times 10\text{ m}$ in each of the analyzed fields. Four grain and straw samples were bulked and dried at 80°C for 10 h, followed by a measurement of nitrogen, phosphorus and potassium by X-ray fluorescence (XRF) spectroscopy (for details see Mäder et al., 2007).

2.7. Statistical analysis

All variables, besides pH-values, were log-transformed ($\log_{10} + 1$) to achieve homogeneity of variance and subsequently analyzed by planned comparisons, using five predefined contrasts:

- CONFYM and CONMIN versus BIOORG and BIODYN (conventional versus organic farming)
- CONMIN versus CONFYM, BIOORG and BIODYN (conventional stockless versus mixed farming)
- CONFYM versus BIOORG and BIODYN (conventional with livestock versus organic farming)
- CONMIN versus CONFYM (conventional stockless versus conventional with livestock)
- BIOORG versus BIODYN (organic farming with composted versus rotted FYM)

Partitioning the between groups sums of squares provided F - and P -values for equal and unequal sample sizes. Data are only presented in figures for variables that significantly differed ($P < 0.05$) for at least one contrast. We further assigned each variable to one of six categories (soil chemistry, microbial biomass, microbial activity, soil fauna, aboveground fauna and plant productivity). The variables of each category were ordinated by principal components analysis (PCA) using CANOCO 4.5. Choice of a linear ordination method was validated by detrended correspondence analysis (DCA) of categories indicating a maximum gradient length below 4 for each category (Ter Braak and Smilauer, 2002). The sample scores of the four PCA axes were further analyzed for individual categories (fixed factor MANOVA) and subsequently treatment effects on categories were analyzed by predefined contrasts as described above.

3. Results

3.1. Soil chemistry

Soil pH ranged from 4.5 to 5.8 in different farming systems; it was lowest in the CONMIN system being 0.7 pH units lower than in the CONFYM system (Fig. 1a). CONFYM and the two organic systems (BIOORG and BIODYN) differed significantly albeit the differences were relatively minor. The BIODYN soils had the highest pH and this was the only difference between BIOORG and BIODYN. Soil organic carbon (C_{org}) and total soil nitrogen (N_{tot}) were lowest in the CONMIN and highest in the BIODYN system (Fig. 1b, c). Soil carbon content increased by 9% from CONMIN to CONFYM, by 8% from CONFYM to BIOORG and by 11% from BIOORG to BIODYN. Soil carbon to nitrogen ratio did not differ significantly between any of

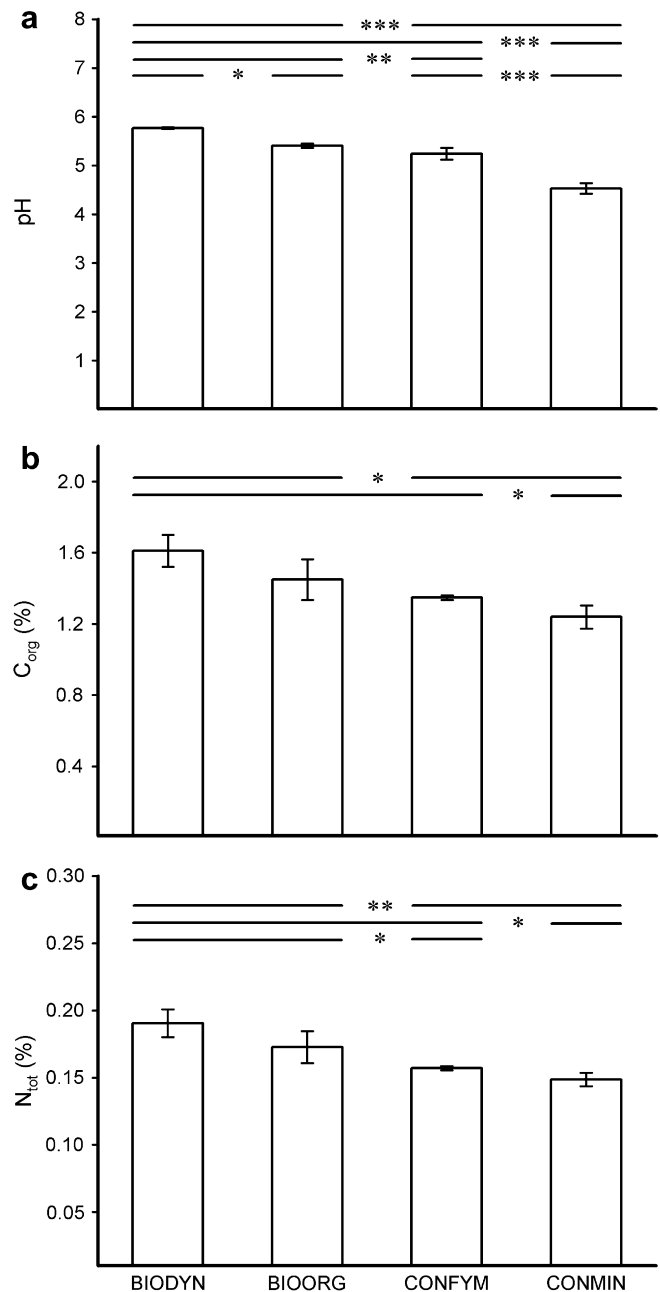


Fig. 1. Arithmetic mean of soil chemical properties: (a) soil pH, (b) organic carbon content (C_{org}), (c) and total nitrogen content (N_{tot}), the latter two expressed in % of the soil dry mass in different farming systems ($N = 4$ per farming system). BIODYN, organic farming with composted manure; BIOORG, organic farming with rotted manure; CONFYM, conventional farming with manure; CONMIN, stockless conventional farming. Significant differences are indicated by contrast analysis; * $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$. Error bars indicate standard errors.

the systems averaging 8.5. Also, soil moisture did not significantly differ between farming systems and was on average 24% of dry weight at the time of sampling.

3.2. Microbial biomass

Microbial biomass parameters increased in the order CONMIN < CONFYM < BIOORG \leq BIODYN (Fig. 2a–f). C_{mic} and N_{mic} significantly separated CONMIN, CONFYM and organic farming systems but not BIOORG and BIODYN (Fig. 2a, b). C_{mic} in BIODYN systems exceeded that in CONMIN systems by more than twofold. This difference was even more pronounced for N_{mic} , with a 2.7-fold

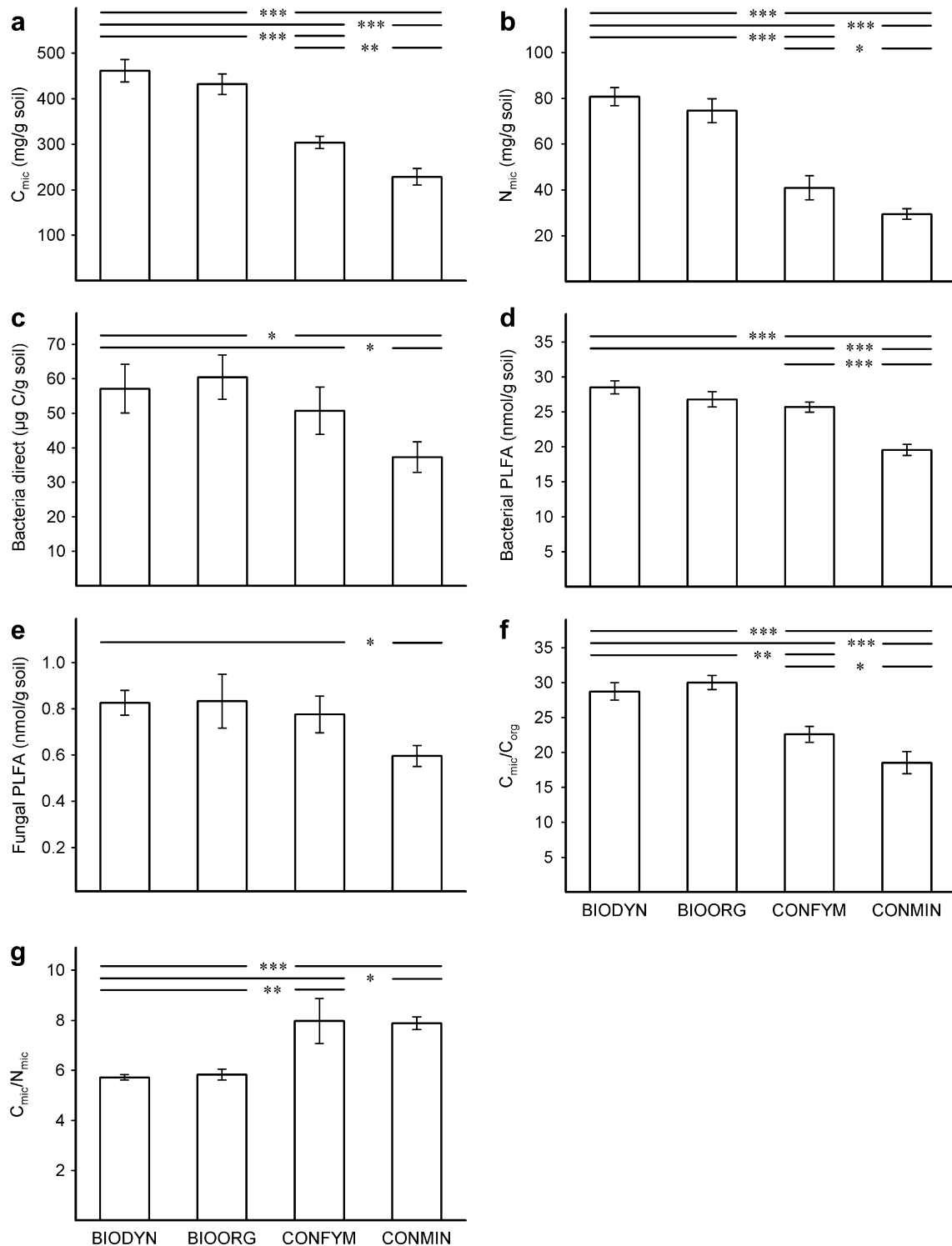


Fig. 2. Arithmetic mean of microbial biomass parameters: (a) microbial biomass carbon (C_{mic}), (b) microbial biomass nitrogen (N_{mic}), (c) bacterial biomass (bacteria direct, fluorescence microscopy), (d) bacterial marker PLFA, (e) fungal marker PLFA, microbial biomass carbon to organic carbon ratio (f) and (g) microbial biomass carbon to microbial biomass nitrogen ratio in different farming systems. For legend see Fig. 1.

increase. Bacterial biomass (fluorescence microscopy; Fig. 2c), bacterial PLFAs and the fungal PLFA 18:2 ω 6 discriminated the CONMIN system from the other farming systems with the CONFYM system being intermediate between the CONMIN and both organic systems (Fig. 2c–e). Bacterial biomass and bacterial PLFA markers were 1.5 times higher in BIODYN as compared to CONMIN; the respective factor for the fungal PLFA 18:2 ω 6 was 1.4. Hyphal

biomass of fungi measured by fluorescence microscopy, including saprotrophic and mycorrhizal fungi (mean of all farming systems 11.7 μ g C g⁻¹ dry wt) and the biomarker for mycorrhizal fungi, NLFA 16:1 ω 5, (4.58 nmol g⁻¹ dry wt) did not differ significantly between farming systems.

The C_{mic} -to- C_{org} ratio was similar in BIOORG and BIODYN systems but significantly higher than in CONFYM and CONMIN

systems (Fig. 2f). The C_{mic} -to- N_{mic} ratio showed an inverse pattern compared to all other microbial biomass parameters. It was similar in the two conventional systems averaging 7.93, but considerably lower in the two organic systems BIOORG and BIODYN averaging 5.77 (Fig. 2g).

3.3. Microbial activity

Microbial basal respiration did not differ significantly between farming systems averaging $2.07 \mu\text{O}_2 \text{g}^{-1} \text{dry wt h}^{-1}$. Due to the similar basal respiration, microbial specific respiration ($q\text{O}_2$) followed an inverse pattern to microbial biomass carbon and N_{mic} (Fig. 3a). In the CONMIN system $q\text{O}_2$ exceeded that in the BIODYN system by a factor of almost two. The ^{14}C maintenance parameter (C_{mnt} ; Fig. 3b) in the CONMIN system significantly exceeded that in

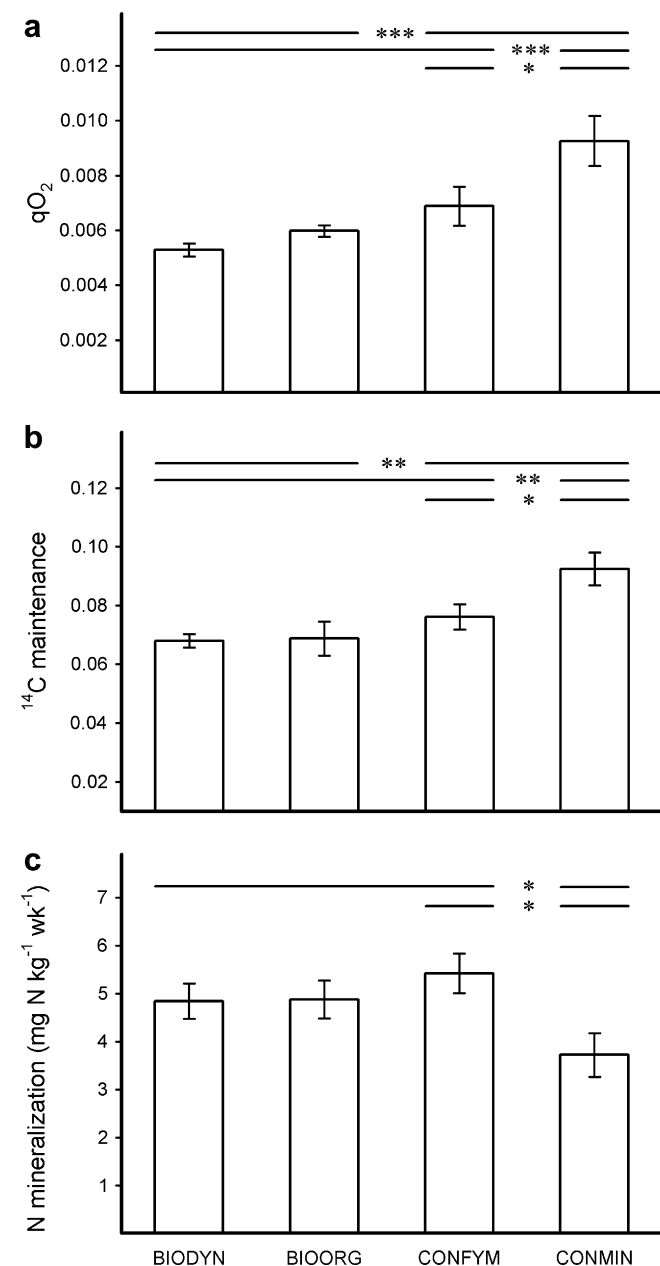


Fig. 3. Arithmetic mean of microbial activity parameters: (a) respiratory quotient ($q\text{O}_2$), (b) ^{14}C maintenance parameter and (c) nitrogen mineralization in different farming systems. For legend see Fig. 1.

each of the other farming systems, in particular BIODYN and BIOORG. Nitrogen mineralization was at a minimum in CONMIN and similar in the other three farming systems receiving farmyard manure (Fig. 3c).

3.4. Soil fauna

Bacterivorous, herbivorous and omnivorous nematodes were about twice as abundant in BIODYN and BIOORG farming systems than in the CONMIN system, while the opposite was true for fungivorous nematodes (Fig. 4a–d, f). Enchytraeids were almost twice as abundant in BIOORG and BIODYN systems as compared to CONMIN and CONFYM (Fig. 4e). Similarly, earthworm abundance was at a maximum in farming systems receiving FYM exceeding that in the CONMIN system by a factor of two (Fig. 4f). Fly larvae (Diptera, Brachycera) were almost absent from CONMIN and CONFYM systems, but reached densities of 116 ind m^{-2} in BIODYN and BIOORG systems (Fig. 4g). Abundance of Protozoa (overall mean $156,382 \text{ ind. g}^{-1} \text{ dry wt}$) and Chilopoda (overall mean 70 ind. m^{-2}) and the generally very low abundance of euedaphic Collembola (1177 ind. m^{-2}) did not differ between farming systems.

3.5. Aboveground fauna and vegetation

Adult web-building spiders were more than twice as abundant in BIODYN and BIOORG as in the two conventional systems (Fig. 5a). Similarly, the density of cursorial spiders was up to 1.8 times higher in the two organic systems (Fig. 5b). As typical for the early growth season, numbers of aphids were generally low. Nevertheless, densities in the two conventional farming systems CONMIN and CONFYM exceeded those in the organic systems BIODYN and BIOORG by a factor of 1.7 (Fig. 5c). Aphid abundance was highest in the CONFYM system. Other surface-active animals, whether predators (Staphylinidae 33 ind. m^{-2} , Carabidae 18 ind. m^{-2}), herbivores (herbivorous beetles 10 ind. m^{-2}) or decomposers (Entomobryidae 50 ind. m^{-2}), did not respond to farming practices. Nematode species richness tended to be higher in both organic systems as compared to the CONMIN system (contrast analysis $F_{1,12} = 4.03$, $P = 0.068$). Neither species richness nor Shannon–Wiener indices differed for other taxa (Enchytraeidae, Araneae and Carabidae).

Grain and straw yields were approximately 23% higher in the two conventional systems, as stand density was 18% lower in both organic systems (Fig. 6a–c). Nitrogen content was 1.2 times higher in grains and 1.9 times higher in straw from conventionally managed fields (Fig. 6d–e). The phosphorus and potassium contents of grains and straw did not differ significantly, with the exception of a 1.5 times higher potassium content of straw from the two conventional systems as compared to both organic plots (Fig. 6f).

3.6. Ordination

Soil chemistry parameters differed significantly between farming systems (Fig. 7a; MANOVA $F_{12,24} = 6.24$, $P < 0.001$) classifying the systems receiving FYM (BIODYN, BIOORG and CONFYM) as significantly different from the stockless conventional system (CONMIN, contrast analysis; Table 2). Further, the two conventional farming systems differed significantly, with the CONFYM system being also significantly different from the two organic systems.

Microbial biomass (Fig. 7b; MANOVA $F_{12,24} = 3.46$, $P = 0.005$) and microbial activity parameters (Fig. 7c; MANOVA $F_{12,24} = 2.35$, $P = 0.036$) also discriminated the organic systems (BIOORG and BIODYN) from the CONMIN system (contrast analysis; Table 2). In contrast to soil chemistry parameters, both microbial biomass and activity did not discriminate the CONFYM from the CONMIN system. Microbial activity parameters also did not separate the CONFYM system from both organic systems.

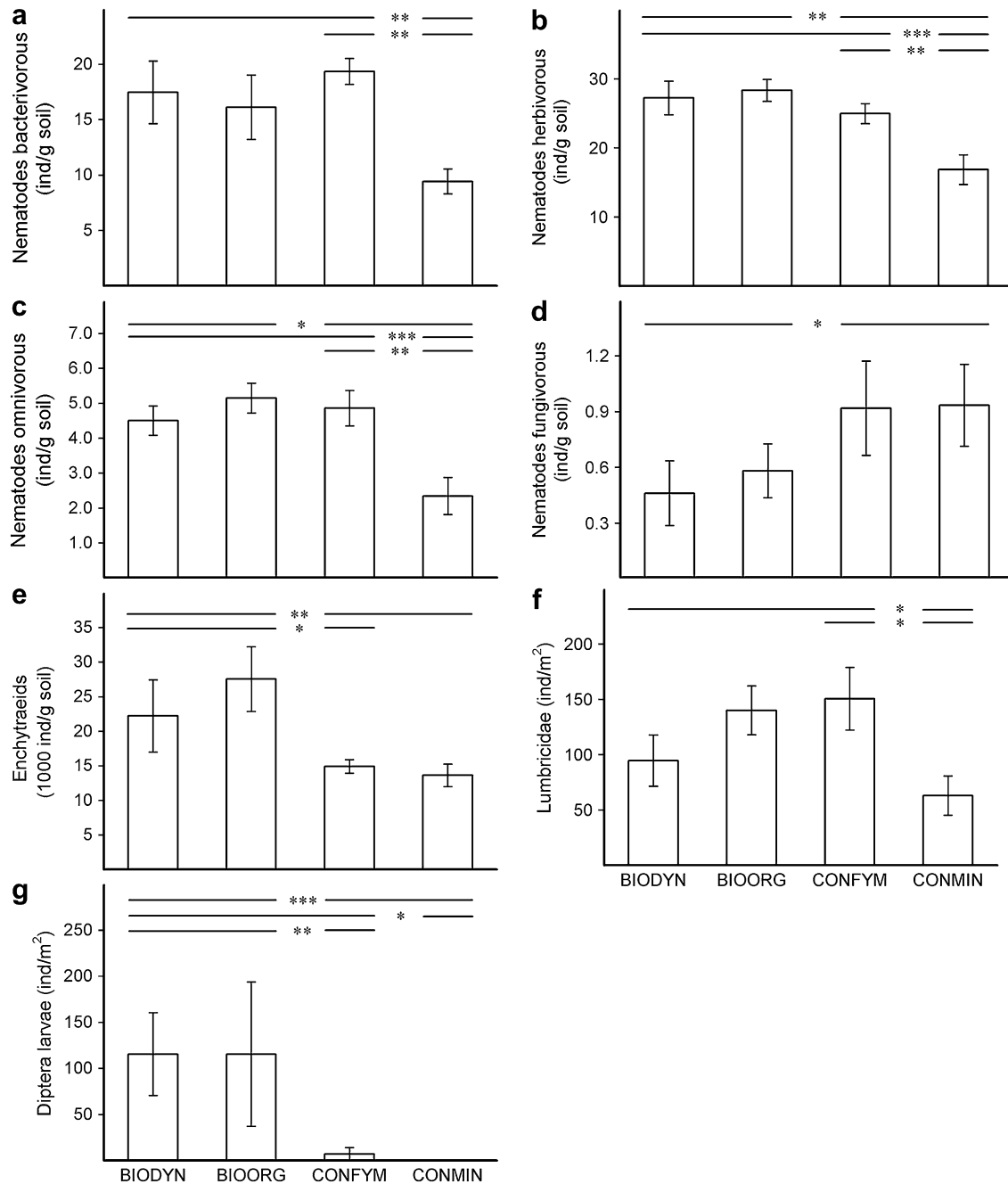


Fig. 4. Arithmetic mean of the soil animal abundance of: (a) bacterivorosus nematodes, (b) herbivorosus nematodes, (c) omnivorosus nematodes, (d) fungivorosus nematodes, (e) enchytraeids, (f) earthworms and (g) Diptera larvae (Brachycera) in different farming systems. For legend see Fig. 1.

The soil fauna community significantly differed between farming systems (Fig. 7d; MANOVA $F_{12,24} = 3.32$, $P = 0.006$), with a highly significant difference between conventional systems (CONFYM and CONMIN) and organic systems (BIOORG and BIODYN; Table 2). The reaction of the soil fauna to different farming systems mirrored the differences in soil chemical parameters, although generally the response was less strong.

Similar to the soil fauna, the aboveground arthropod community differed significantly between conventional managed fields and those receiving organic fertilizers, although the difference was less pronounced (Fig. 7e; MANOVA $F_{12,24} = 2.38$, $P = 0.034$). Aboveground fauna was the only analyzed category that did not significantly separate the CONMIN from the other systems. Plant data discriminated both organic systems from the conventionally

managed fields (Fig. 7f; MANOVA $F_{12,24} = 6.27$, $P < 0.001$) and mirrored the response of the soil fauna.

4. Discussion

The farming systems investigated differed markedly in plant productivity, chemical, microbial and faunal properties. The analyzed parameters suggest improved soil quality and a higher pest resilience in organic systems compared to systems receiving mineral fertilizers and pesticides, in particular to the system receiving only mineral nutrients (CONMIN). In addition to general differences between conventional and organic farming systems, abiotic soil properties, soil fauna composition and plant productivity also separated the two conventional systems. Organic systems, either

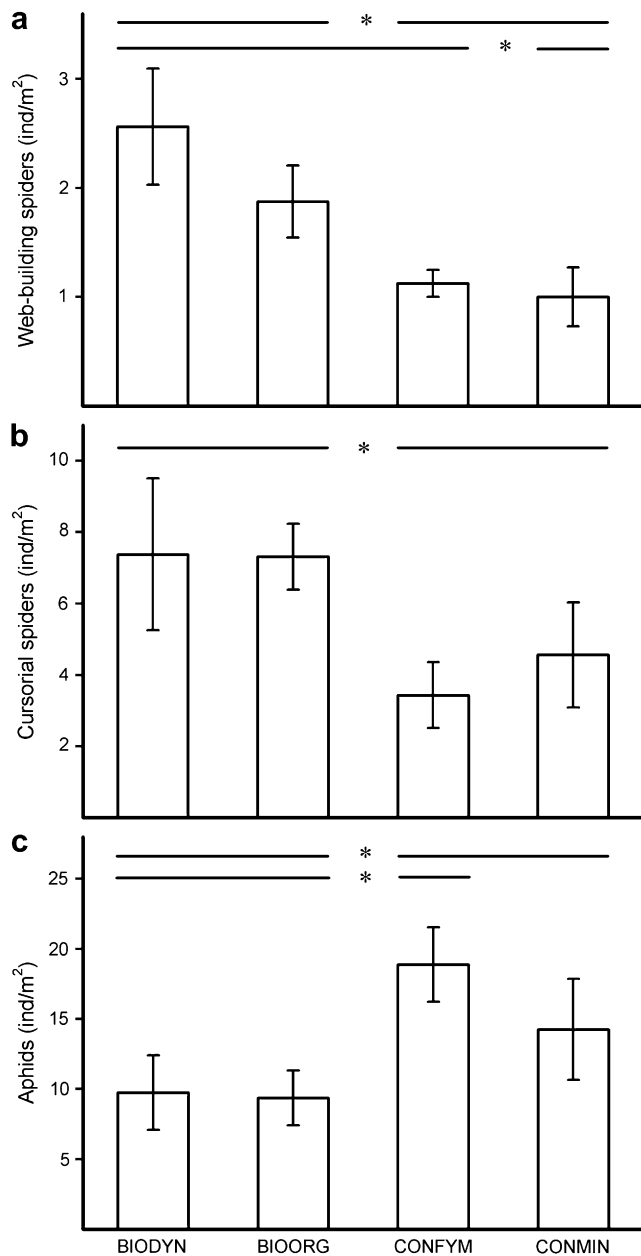


Fig. 5. Arithmetic mean of aboveground animal abundance of: (a) adult web-building spiders, (b) adult cursorial spiders and (c) aphids in different farming systems. For legend see Fig. 1.

receiving composted or rotted manure did not differ for the analyzed parameters.

4.1. Soil chemistry

Soil organic carbon (C_{org}) and total soil nitrogen content (N_{tot}) were 18–19% higher in both organic systems than in the conventional systems, whereas there were no significant differences between the two conventional systems. Since one conventional (CONFYM) and one organic system (BIOORG) received equivalent amounts of organic carbon over the last 27 years, the long-term application of additional mineral fertilizer and/or pesticides likely counteracted the build-up of carbon rich soils. This observation supports earlier findings that mineral N addition increases the decomposition rate of organic residues by satisfying N requirements of microorganisms (Jenkinson et al., 1985). Fließbach

et al. (2007) studied the long-term development of soil organic matter in the DOK trial and found soil organic matter levels to remain relatively stable in the BIODYN system, whereas they were decreasing in all other systems. A lower pH in conventional systems (particularly CONMIN) and the significant loss of soil organic carbon might be explained by the use of acidifying mineral fertilizers. Mineral (NPK) fertilizer application may reduce soil aggregate stability and therefore the protection of soil organic matter in microaggregates (Mikha & Rice, 2004). This may also apply to the conventional systems in the DOK trial, where aggregate stability is higher in organic systems (Mäder et al., 2002). The only analyzed variable that was significantly different between the two organic systems was pH, probably a consequence of the application of a biodynamic preparation (pebble with horsetail) shortly before our sampling.

4.2. Microbial biomass and activity

Similar to soil chemical properties, microbial biomass parameters separated the CONFYM system from both organic systems. Despite receiving similar amounts of organic fertilizer as the BIOORG system, microbial biomass was 30% lower in this system whereas nitrogen mineralization rates were on average 10% higher. The stockless conventional system CONMIN showed a similar pattern with both C_{mic} and N_{mic} being lower than in organic systems, while microbial activity was higher. This suggests that soil carbon in the conventional systems is more easily accessible to microorganisms than in both organic systems. In the organic systems carbon tied-up in microbial biomass is increased but higher microbial biomass is associated with reduced losses through respiration (see also Fließbach and Mäder, 2000). Presumably, due to the availability of nutrients in excess, the structure of the microbial community in the conventional systems shifted dominance towards early successional species with high turnover rates at the expense of competitive species with more efficient resource use.

The fungal and bacterial PLFA markers were increased by 17–18% in systems receiving FYM as compared to the CONMIN system. Wander et al. (1995) reported no significant difference in the PLFA profile comparing different agricultural management systems, whereas O'Donnell et al. (2001) identified differences between treatments receiving either FYM and inorganic fertilizer or NPK fertilizer only. Results of our study suggest long-term consequences of farming systems for microorganisms with bacteria and fungi increasing in biomass by the addition of organic fertilizers, even if applied in combination with mineral fertilizers and herbicides (CONFYM). Bacterial biomass (direct microscopy) showed the same pattern as microbial biomass (C_{mic}) and bacterial PLFAs. However, bacterial biomass as measured by image analysis represented only 12–15% of microbial biomass; similar ratios have been reported before (Jenkinson et al., 1976).

4.3. Soil fauna

Among microfauna, bacterivorous and plant feeding nematodes dominated in each of the systems; fungivorous nematodes were far less abundant. Despite their low abundance, fungivorous nematode densities were 43% higher in the two conventional systems than in the organic systems. This was unexpected since fungal marker PLFA indicates low fungal biomass in the CONMIN system and fungivorous nematodes in grasslands are assumed to be more sensitive to intensive farming practices than bacterial feeders (Mulder et al., 2003). Presumably, the fungi dominating in the conventional systems were of high food quality, or the fungivorous nematodes used alternative food sources such as root hairs (Yeates and Bongers, 1999). In contrast to fungivorous nematodes, the densities of omnivorous nematodes and enchytraeids were lowest in the CONMIN

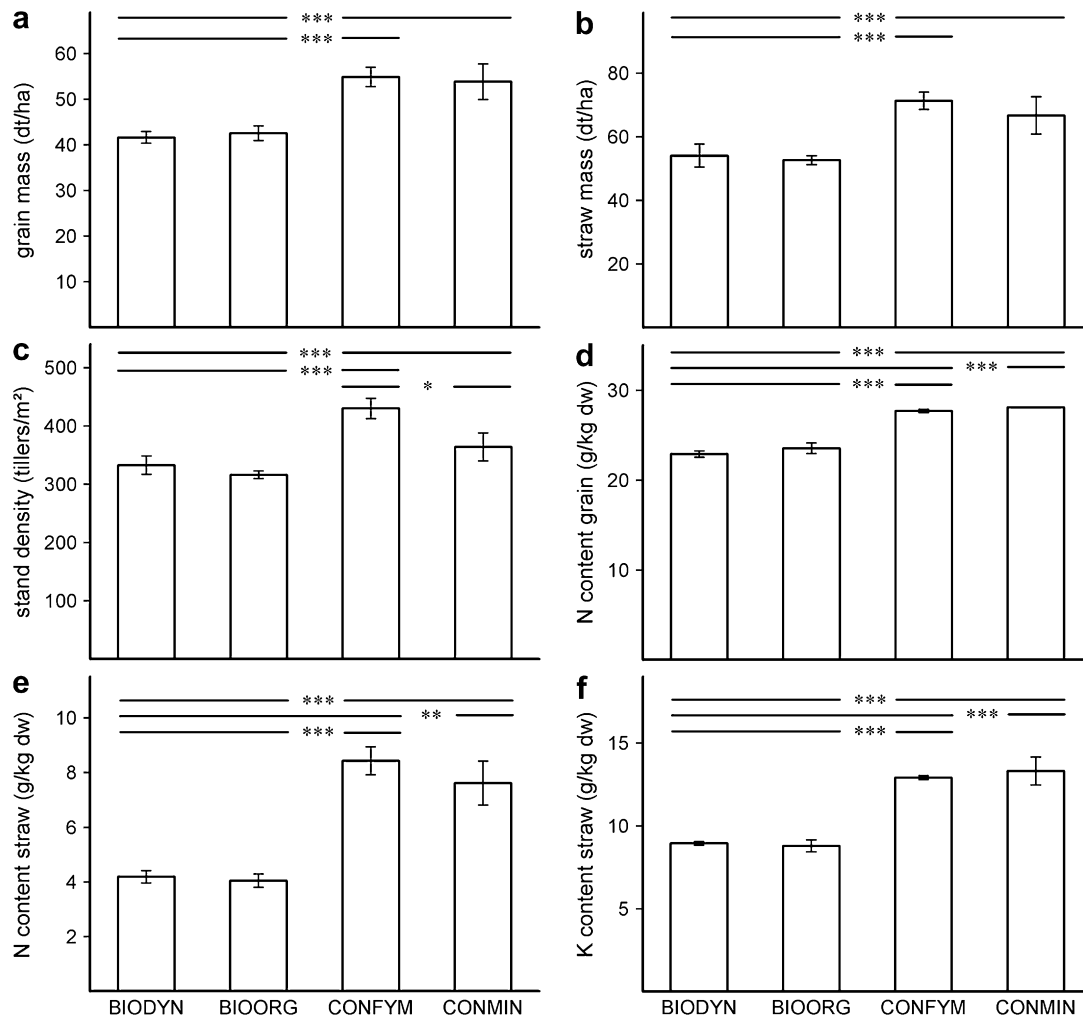


Fig. 6. Arithmetic mean of (a) grain biomass, (b) straw biomass, (c) wheat stand density, (d) N content of grains, (e) N content of straw and (f) K content of straw. For legend see Fig. 1.

system. Assuming that omnivorous nematodes live on microorganisms and organic residues, this is consistent with low microbial biomass and lack of organic input to this system. Compared to the conventional systems herbivorous nematodes were on average 33% more abundant in both organic systems suggesting that they benefited from an increased root system resulting from root nutrient foraging in the organic systems (Andrzejewska, 1976).

Herbicides and the molluscicide applications in 2003 and 2004 did not have detectable negative impact on earthworms and nematodes, as the density of earthworms and the three most abundant nematode feeding groups did not differ between the CONFYM system which received pesticides and the organic systems which did not. Similarly, Iglesias et al. (2003) reported that even high doses of molluscicides (metaldehyde pellets) did not negatively affect soil animal communities.

Nematode communities tended to be more diverse in systems receiving FYM. However, differences were not statistically significant and suggest that decomposer diversity in general responds little to the input of more complex litter resources (Wardle, 2005). Earthworms benefited from organic fertilizer (cf. Piffner, 1993) and the increased abundance might have contributed to the enhanced microbial activity and biomass through incorporation of litter materials into the soil (Tiunov and Scheu, 2000). Density of Diptera larvae and enchytraeids was higher in both organic systems. This suggests that NPK fertilizer and/or pesticide application in the

CONFYM system suppressed Diptera and enchytraeids. In fact, Salminen et al. (1996) showed that mortality rates of enchytraeids are high when exposed to a commercial herbicide preparation.

4.4. Aboveground fauna and vegetation

Aphids were almost twice as abundant in systems which received mineral fertilizer and herbicides (CONMIN and CONFYM). It is known that aphid development heavily relies on plant nitrogen supply (Schütz et al., 2008) and increased nitrogen concentration in conventionally managed crops therefore likely results in higher aphid abundance (Nevo and Coll, 2001). Our data support this prediction as aphid densities increased with the nitrogen concentration of wheat plants ($N = 16$, $r = 0.715$, $P = 0.002$).

The predator community was dominated by spiders, and staphylinid and carabid beetles, but only spiders responded to farming systems. Web-building spiders attach their webs to the vegetation and therefore benefit from increased availability of suitable web sites (Birkhofer et al., 2007). Increased activity-density of web-building spiders in organically managed systems therefore often is attributed to higher weed coverage (Schmidt et al., 2005). As weed growth suffers from herbicide application and increased wheat stand density, a negative response to conventional management may explain the lower abundance of web-builders in our conventional systems. However, our sampling took part early in

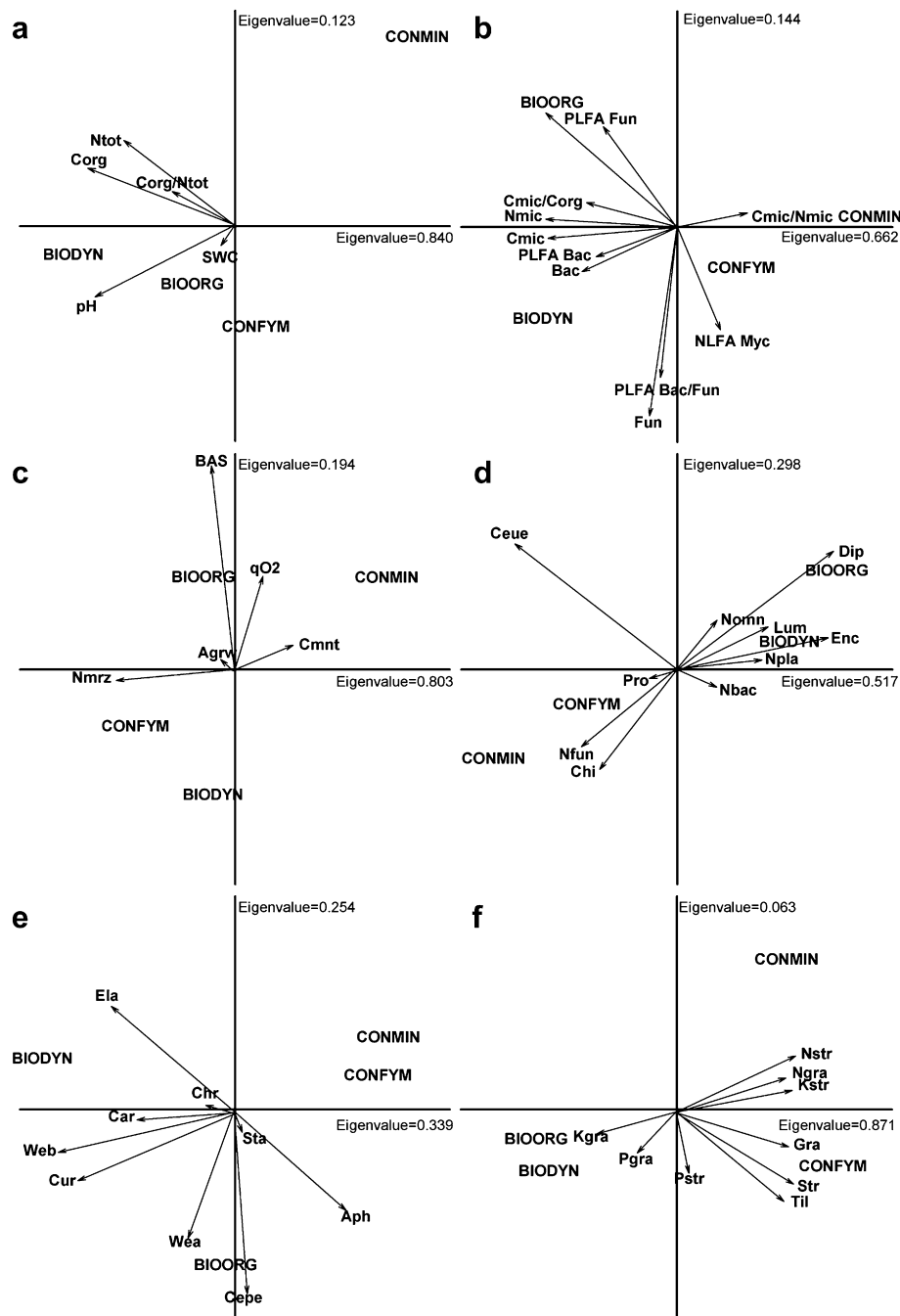


Fig. 7. Principal components analysis for five parameter categories (a–f), showing sample scores of all analyzed variables per category and treatment positions as centroids (log-transformed data). For treatments see Table 1. (a) Soil chemistry C_{org} , organic carbon content; C_{org}/N_{tot} , organic carbon to nitrogen ratio; N_{tot} , total nitrogen content; pH, soil pH; SWC, soil water content; (b) microbial biomass Bac, bacterial biomass (fluorescence microscopy); C_{mic} , microbial biomass carbon; C_{mic}/C_{org} , ratio microbial biomass carbon to organic carbon content; C_{mic}/N_{mic} , ratio microbial biomass carbon to microbial biomass nitrogen; Fun, fungal biomass (fluorescence microscopy); NLFA_{Myc}, mycorrhizal marker NLFA; N_{mic} , microbial biomass nitrogen; PLFA_{Bac/Fun}, ratio bacterial PLFA to fungal PLFA; PLFA_{Bac}, bacterial marker PLFA; PLFA_{Fun}, fungal marker PLFA; (c) microbial activity A_{grw} , ^{14}C growth parameter; BAS, basal respiration; C_{mnt} , ^{14}C maintenance parameter; N_{mrz} , nitrogen mineralization; qO_2 , respiratory quotient; (d) soil fauna Dip, Diptera larvae; Chi, Chilopoda; C_{eue} , euedaphic Collembola; Enc, Enchytraeidae; Lum, Lumbricidae; N_{fun} , fungivorous Nematodes; N_{pla} , herbivorous Nematodes; N_{omn} , omnivorous Nematodes; N_{bac} , bacterivorous Nematodes; Pro, Protozoa; (e) aboveground fauna Aph, Aphids; Car, Carabidae; Chr, Chrysomelidae; C_{epe} , epedaphic Collembola; Cur, cursorial spiders; Ela, Elateridae; Sta, Staphylinidae; Wea, Curculionidae (Weavils); Web, web-building spiders; (f) plants K_{gra} , potassium content grains; K_{str} , potassium content straw; N_{gra} , nitrogen content grains; N_{str} , nitrogen content straw; P_{gra} , phosphor content grains; P_{str} , phosphor content straw; Gra, biomass grains; Str, biomass straw; Til, wheat stand density.

the growing season and weed growth was generally limited (personal observation). Similar to web-building spiders, the activity-density of surface-active spiders was increased in organic wheat systems. Comparable results were found in organically managed grass–clover systems in the DOK trial (Birkhofer et al., in press); however, pest suppression was not enhanced by higher generalist predator numbers in those grasslands.

Diptera larvae mirrored the response of spiders to organic fertilization suggesting a numerical response of spiders to this soil-based prey (cf. Harwood et al., 2007). Some spider species prey frequently on aphids, as indicated by recent molecular studies (Harwood et al., 2004) and field experiments (Birkhofer et al., 2008b). Östman et al. (2001) demonstrated that aphids were more successfully suppressed by natural enemies in organic as compared

Table 2

Contrast comparison based on fixed factor MANOVA results using sample scores of four axes from PCA for each parameter category (a–f)

Contrast	Soil chemistry		Microbial biomass		Microbial activity		Soil fauna		Aboveground fauna		Plants	
	$F_{4,9}$	<i>P</i>	$F_{4,9}$	<i>P</i>	$F_{4,9}$	<i>P</i>	$F_{4,9}$	<i>P</i>	$F_{4,9}$	<i>P</i>	$F_{4,9}$	<i>P</i>
a	28.81	<0.001	20.36	<0.001	5.11	0.019	6.57	0.009	5.34	0.018	37.70	<0.001
b	35.55	<0.001	14.98	<0.001	7.17	0.007	5.45	0.016	1.01	0.450	20.51	<0.001
c	7.25	0.006	7.85	0.005	1.48	0.287	5.55	0.016	5.55	0.016	5.98	0.012
d	13.98	<0.001	2.47	0.119	3.53	0.054	4.43	0.030	1.22	0.368	3.67	0.049
e	2.83	0.090	0.51	0.728	0.91	0.498	0.54	0.711	2.59	0.108	0.32	0.859

Contrasts were specified to compare different farming systems: (a) CONFYM and CONMIN versus BIOORG and BIODYN (conventional versus organic farming) (b) CONMIN versus CONFYM, BIOORG and BIODYN (stockless farming versus mixed farming) (c) CONFYM versus BIOORG and BIODYN (conventional with livestock versus organic farming) (d) CONMIN versus CONFYM (conventional stockless versus conventional with livestock) and (e) BIOORG versus BIODYN (organic farming with rotted versus composted FYM).

to conventional farming systems. In addition to increased nutrient availability, reduced spider abundance therefore likely contributed to the high density of aphids in systems receiving mineral fertilizers. Our results therefore support the assumption of improved pest suppression in organic farming systems (Zehnder et al., 2007). Overall, the investigated farming systems affected the aboveground fauna including herbivore pest species, even though effects were less pronounced than in the belowground system. This less pronounced response may have resulted from small plot size since aboveground invertebrates are more mobile than soil fauna. Effects of farming systems on aboveground invertebrates likely resulted from both, increased nutrient supply to plants in conventional systems and fostering of herbivore control by generalist predators in organic farming systems.

Wheat yield was on average 23% lower in organic farming systems in 2005 which corresponds to previous long-term investigations (Mäder et al., 2007). The 31% higher addition of nitrogen to conventionally managed systems resulted in 49% higher nitrogen content in wheat straw. Despite the reduced aboveground productivity of plants in organic farming systems, negative consequences, such as reduced soil quality and increased herbivore pest susceptibility, may outweigh economic benefits of conventional farming (for long-term yield data see Mäder et al., 2002).

5. Conclusions

Long-term organic farming and the application of farmyard manure promoted soil quality, microbial biomass and fostered natural enemies and ecosystem engineers, suggesting enhanced nutrient cycling and pest resilience. Application of farmyard manure increased the resource basis for belowground communities and beneficially affected the activity and biomass of decomposer biota. Mineral fertilizers and herbicide application, in contrast, affected the potential for top-down control of aboveground pests negatively and reduced the organic carbon levels. The combined application of mineral and organic fertilizers appeared to counteract beneficial effects of organic fertilizers, such as enhanced microbial biomass or reduced pest abundance. Our comprehensive study indicates that organic fertilizers foster biotic interactions within and between below and aboveground components thereby improving the sustainability of farming systems.

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References

- Andrzejewska, L., 1976. The influence of mineral fertilization on the meadow phytophagous fauna. *Polish Ecological Studies* 2, 93–109.
- Bengtsson, J., Ahnstrom, J., Weibull, A.C., 2005. The effects of organic agriculture on biodiversity and abundance: a meta-analysis. *Journal of Applied Ecology* 42, 261–269.
- Birkhofer, K., Scheu, S., Wise, D.H., 2007. Small-scale spatial pattern of web-building spiders (Araneae) in alfalfa: relationship to disturbance from cutting, prey availability, and intraguild interaction. *Environmental Entomology* 36, 801–810.
- Birkhofer, K., Wise, D.H., Scheu, S., 2008a. Subsidy from the detrital food web, but not microhabitat complexity, affects the role of generalist predators in an aboveground herbivore food web. *Oikos* 117, 494–500.
- Birkhofer, K., Gavish-Regev, E., Endlweber, K., Lubin, Y.D., von Berg, K., Wise, D.H., Scheu, S., 2008b. Cursorial spiders retard initial aphid population growth at low densities in winter wheat. *Bulletin of Entomological Research* 98, 249–255.
- Birkhofer, K., Fließbach, A., Wise, D.H., Scheu, S. Generalist predators in organically and conventionally managed grass–clover fields: implications for conservation biological control. *Annals of Applied Biology*, in press. doi:10.1111/j.1744-7348.2008.00257.x.
- Bloem, J., Vos, A., 2004. Fluorescent staining of microbes for total direct counts. In: Kowalchuk, G.A., de Bruijn, F.J., Head, I.M., Akkermans, A.D.L., van Elsas, J.D. (Eds.), *Molecular Microbial Ecology Manual*. Kluwer Academic Publishers, Dordrecht, pp. 861–874.
- Bloem, J., Veninga, M., Shepherd, J., 1995. Fully automatic determination of soil bacterium numbers, cell volumes and frequencies of dividing cells by confocal laser scanning microscopy and image analysis. *Applied and Environmental Microbiology* 61, 926–936.
- Bongers, T., 1988. *De Nematoden van Nederland*. Pirola, Schoorl.
- Curtin, D., Wright, C.E., Beare, M.H., McCallum, F.M., 2006. Hot water-extractable nitrogen as an indicator of soil nitrogen availability. *Soil Science Society of America Journal* 70, 1512–1521.
- Dunger, W., Fiedler, H.J., 1997. *Methoden der Bodenbiologie*. Gustav Fischer Verlag, Jena.
- Fließbach, A., Mäder, P., 2000. Microbial biomass and size-density fractions differ between soils of organic and conventional agricultural systems. *Soil Biology and Biochemistry* 32, 757–768.
- Fließbach, A., Oberholzer, H.R., Gunst, L., Mäder, P., 2007. Soil organic matter and biological soil quality indicators after 21 years of organic and conventional farming. *Agriculture, Ecosystem and Environment* 118, 273–284.
- Forster, J.C., 1995. Soil physical analysis. In: Alef, K., Nannipieri, P. (Eds.), *Methods in Applied Soil Microbiology and Biochemistry*. Academic Press, San Diego, pp. 105–122.
- Frostegård, Å., Bååth, E., 1996. The use of phospholipid fatty acid analysis to estimate bacterial and fungal biomass in soil. *Biology and Fertility of Soils* 22, 59–65.
- Frostegård, Å., Tunlid, A., Bååth, E., 1993. Phospholipid fatty acid composition, Biomass and activity of microbial communities from two soil types experimentally exposed to different heavy metals. *Applied Environmental Microbiology* 59, 3605–3617.
- Halaj, J., Wise, D.H., 2002. Impact of a detrital subsidy on trophic cascades in a terrestrial grazing food web. *Ecology* 83, 3141–3151.
- Harwood, J.D., Sunderland, K.D., Symondson, W.O.C., 2004. Prey selection by linyphiid spiders: molecular tracking of the effects of alternative prey on rates of aphid consumption in the field. *Molecular Ecology* 13, 3549–3560.
- Harwood, J.D., Bostrom, M.R., Hladilek, E.E., Wise, D.H., Obrycki, J.J., 2007. An order-specific monoclonal antibody to Diptera reveals the impact of alternative prey on spider feeding behaviour in a complex food web. *Biological Control* 41, 397–407.
- Hedlund, K., 2002. Soil microbial community structure in relation to plant diversity management on former agricultural land. *Soil Biology and Biochemistry* 34, 1299–1307.
- Iglesias, J., Castillejo, J., Castro, R., 2003. The effects of repeated applications of the molluscicide metaldehyde and the biocontrol nematode *Phasmarhabditis hermaphrodita* on molluscs, earthworms, nematodes, acarids and collembolans: a two-year study in north-west Spain. *Pest Management Science* 59, 1217–1224.
- Jenkinson, D.S., Powelson, D.S., Wedderburn, R.W.M., 1976. The effects of biocidal treatments on metabolism in soil-III. The relationship between soil biovolume, measured by optical microscopy, and the flush of decomposition caused by fumigation. *Soil Biology and Biochemistry* 8, 189–202.

- Jenkinson, D.S., Fox, R.H., Rayner, J.H., 1985. Interactions between fertilizer nitrogen and soil-nitrogen – the so-called priming effect. *Journal of Soil Science* 36, 425–444.
- Kempson, D., Lloyd, M., Ghelardi, R., 1963. A new extractor for woodland litter. *Pedobiologia* 3, 1–21.
- Letourneau, D.K., Bothwell, S.G. Comparison of organic and conventional farms: challenging ecologists to make biodiversity functional. *Frontiers in Ecology and the Environment*, in press.
- Lundquist, E.J., Jackson, L.E., Scow, K.M., Hsu, C., 1999. Changes in microbial biomass and community composition, and soil carbon and nitrogen pools after incorporation of rye into three California agricultural soils. *Soil Biology and Biochemistry* 31, 221–236.
- Mäder, P., Fließbach, A., Dubois, D., Gunst, L., Fried, P., Niggli, U., 2002. Soil fertility and biodiversity in organic farming. *Science* 296, 1694–1697.
- Mäder, P., Hahn, D., Dubois, D., Gunst, L., Alföldi, T., Bergmann, H., Oehme, M., Amadó, T., Schneider, H., Graf, U., Velimirov, A., Fließbach, A., Niggli, U., 2007. Wheat quality in organic and conventional farming: results of a 21 year field experiment. *Journal of the Science of Food and Agriculture* 87, 1826–1837.
- Mikha, M.M., Rice, C.W., 2004. Tillage and manure effects on soil and aggregate-associated carbon and nitrogen. *Soil Science Society of America Journal* 68, 809–816.
- Mulder, C., De Zwart, D., Van Wijnen, H.J., Schouten, A.J., Breure, A.M., 2003. Observational and simulated evidence of ecological shifts within the soil nematode community of agroecosystems under conventional and organic farming. *Functional Ecology* 17, 516–525.
- Nevo, E., Coll, M., 2001. Effects of nitrogen fertilization on *Aphis gossypii* (Homoptera: Aphididae): variation in size, color, and reproduction. *Journal of Economic Entomology* 94, 27–32.
- Nguyen, C., Henry, F., 2002. A carbon-14-glucose assay to compare microbial activity between rhizosphere samples. *Biology and Fertility of Soils* 35, 270–276.
- O'Connor, F.B., 1955. Extraction of enchytraeid worms from a coniferous forest soil. *Nature* 175, 815–816.
- O'Donnell, O.G., Seasman, M., Macrae, A., Waite, L., Davies, J.T., 2001. Plants and fertilisers as drivers of change in microbial community structure and function in soils. *Plant and Soil* 232, 135–145.
- Oehl, F., Sieverding, E., Mader, P., Dubois, D., Ineichen, K., Boller, T., Wiemken, A., 2004. Impact of long-term conventional and organic farming on the diversity of arbuscular mycorrhizal fungi. *Oecologia* 138, 574–583.
- Oksanen, L., Aunapuu, M., Oksanen, T., Schneider, M., Ekerholm, P., Lundberg, P.A., Armulik, T., Aruoja, V., Bondstad, L., 1997. Outlines of food webs in a low arctic tundra landscape in relation to three theories on trophic dynamics. In: Gange, A.C., Brown, V.K. (Eds.), *Multitrophic Interactions in Terrestrial Systems*. Blackwell Science, Oxford, pp. 351–373.
- Olsson, P.A., 1999. Signature fatty acids provide tools for determination of the distribution and interactions of mycorrhizal fungi in soil. *FEMS Microbiology Ecology* 29, 303–310.
- Oostenbrink, M., 1960. Estimating nematode populations by some selected methods. In: Sasser, N.J., Jenkins, W.R. (Eds.), *Nematology*. University of North Carolina Press, Chapel Hill, pp. 85–102.
- Östman, O., Ekblom, B., Bengtsson, J., 2001. Landscape heterogeneity and farming practice influence biological control. *Basic and Applied Ecology* 2, 365–371.
- Page, F.C., 1988. *A New Key to Freshwater and Soil Gymnamoebae*. Freshwater Biological Association, Ambleside.
- Pfiffner, L., 1993. Long-term effect of biological and conventional farming on earthworm populations. *Journal of Plant Nutrition and Soil Science* 156, 259–265.
- Rasmussen, P.E., Goulding, K.W.T., Brown, J.R., Grace, P.R., Janzen, H.H., Körschens, M., 1998. Long-term agroecosystem experiments: assessing agricultural sustainability and global change. *Science* 282, 893–896.
- Rønn, R., Ekelund, F., Christensen, S., 1995. Optimizing soil extract and broth media for MPN-enumeration of naked amoebae and heterotrophic flagellates in soil. *Pedobiologia* 39, 10–19.
- Ryan, M., 1999. Is an enhanced soil biological community, relative to conventional neighbours, a consistent feature of alternative (organic and biodynamic) agricultural systems? *Biological Agriculture and Horticulture* 17, 131–144.
- Salminen, J., Eriksson, I., Haimi, J., 1996. Effects of terbutylazine on soil fauna and decomposition processes. *Ecotoxicology and Environmental Safety* 34, 184–189.
- Scheu, S., 1992. Automated measurement of the respiratory response of soil microcompartments: active microbial biomass in earthworm faeces. *Soil Biology and Biochemistry* 24, 1113–1118.
- Scheu, S., 2001. Plants and generalist predators as links between the below-ground and above-ground system. *Basic and Applied Ecology* 2, 3–13.
- Schmidt, M.H., Roschewitz, I., Thies, C., Tscharrntke, T., 2005. Differential effects of landscape and management on diversity and density of ground-dwelling farmland spiders. *Journal of Applied Ecology* 42, 281–287.
- Schütz, K., Bonkowski, M., Scheu, S., 2008. Effects of Collembola and fertilizers on plant performance (*Triticum aestivum*) and aphid reproduction (*Rhopalosiphum padi*). *Basic and Applied Ecology* 9, 182–188.
- Ter Braak, C.J.F., Smilauer, P., 2002. *CANOCO Reference Manual and CanoDraw for Windows User's Guide: Software for Canonical Community Ordination (Version 4.5)*. Microcomputer Power, New York.
- Tiunov, A.V., Scheu, S., 2000. Microbial biomass, biovolume and respiration in *Lumbricus terrestris* L. cast material of different age. *Soil Biology and Biochemistry* 32, 265–275.
- Tivy, J., 1987. Nutrient cycling in agro-ecosystems. *Applied Geography* 7, 93–113.
- Vance, E.D., Brookes, P.D., Jenkinson, D.S., 1987. An extraction method for measuring soil microbial biomass carbon. *Soil Biology and Biochemistry* 19, 703–708.
- Wander, M.M., Hedrick, D.S., Kaufman, D., Traina, S.J., Stinner, B.R., Kehrmeier, S.R., White, D.C., 1995. The functional significance of the microbial biomass in organic and conventionally managed soils. *Plant and Soil* 170, 87–97.
- Wardle, D.A., 2002. *Communities and Ecosystems: Linking the Aboveground and Belowground Components*. Princeton University Press, Princeton.
- Wardle, D.A., 2005. How plant communities influence decomposer communities. In: Bardgett, R., Usher, M.B., Hopkins, D.W. (Eds.), *Biological Diversity and Function in Soils*. Cambridge University Press, Cambridge, pp. 119–138.
- Yeates, G.W., Bongers, T., 1999. Nematode diversity in agroecosystems. *Agriculture, Ecosystems and Environment* 74, 113–135.
- Yeates, G.W., Bongers, T., De Goede, R.G.M., Freckman, D.W., Georgieva, S.S., 1993. Feeding-habits in soil nematode families and genera – an outline for soil ecologists. *Journal of Nematology* 25, 315–331.
- Zehnder, G., Gurr, G.M., Kuhne, S., Wade, M.R., Wratten, S.D., Wyss, E., 2007. Arthropod pest management in organic crops. *Annual Review of Entomology* 52, 57–80.